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Short Communication

Unusual importance of insectivory in the diet of the Neotropical otter, *Lontra annectens* (Major, 1897) (Mammalia, Carnivora)

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Abstract

The Neotropical otter, *Lontra annectens*, is a predator specialized in aquatic prey, and the main diet of this otter is fish, supplemented mainly by crustaceans and opportunistically by mollusks, insects, and vertebrates such as mammals, amphibians, birds, and reptiles. Occasionally, they eat fruits. This study was conducted on the El Despoblado River near Villa Comaltitlán, in southern Chiapas. We carried out monthly visits along the riverbanks to collect otter scats from April 2018 to April 2019 and found that insects make up more than half of the diet of otters living in this river. Although insects are a common food in the diet of Neotropical otters, the abundant presence of hellgrammites (dobsonfly larvae; Insecta, Megaloptera) had not been recorded before. Otters were found to consume hellgrammites, which are abundant, easy to catch, and have a high nutritional value. This is probably due to the scarce availability of fish and crustaceans in this part of Chiapas.

Key words: Chiapas, diet, dobsonflies, hellgrammites, insects, Neotropical otter, opportunistic feeding

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Introduction

Neotropical otters are carnivorous mammals adapted to live in aquatic environments, thriving in freshwater habitats such as rivers, streams, and lagoons. They occur even in habitats affected by anthropogenic activities, including sewage systems, artificial lakes, and areas adjacent to human settlements. Several morphological features facilitate their life in water, such as a short and dense coat, a small and flat head with a neck thicker than the head, small eyes and short, rounded ears, a long tail approximately one-third of the total body length, and short legs and webbed fingers (Gallo-Reynoso 1989; Emmons 1990; Emmons and Feer 1997; Larivière 1999).

Most of the available information about the Neotropical otters has been recorded from indirect data, such as scats, scratches, and footprints, rather than from live animals. This information has been used to investigate the distribution, abundance, spatial habitat use, diet, genetic diversity, and overall ecology of Neotropical otters (Gallo-Reynoso 1986; MacDonald and Mason 1992; Pardini 1998; Pardini and Trajano 1999; Quadros and Monteiro-Filho 2001, 2002).

Knowledge of feeding habits is particularly important to understanding otter ecology, as diet has been shown to affect spatial behavior, distribution, activity time, body size, and reproduction, among other aspects (Gittleman 1985; Iriarte et al. 1990; Estes et al. 2003; Swenson et al. 2007).

The diet of Neotropical otters has been extensively studied, and they are probably the carnivores for which the diet is best known (Gallo-Reynoso 1997; Gallo-Reynoso et al. 2008; Pérez-Claros and Palmqvist 2008; Monroy-Vilchis and Mundo 2009; Rangel-Aguilar and Gallo-Reynoso 2013; Rheingantz et al. 2017; Grajales-García et al. 2019). These species are top predators in freshwater ecosystems and good bioindicators of the presence of fish, crustaceans, mollusks, and insects on which they feed (Gallo-Reynoso 1989; García-Silva et al. 2021; Ramos-Rosas et al. 2013). They are considered umbrella species that are afforded protection and serve to protect a wide variety of other species, and their presence in a waterbody indicates the good conservation status of the aquatic environment (García-Silva et al. 2021; Gómez et al. 2014).

Neotropical otters are facultative predators specialized in aquatic prey (Pardini 1998; Quadros and Monteiro-Filho 2001; Rheingantz et al. 2012; 2017), which mainly consists of fish, and, secondarily, crustaceans (Quadros and Monteiro-Filho 2001; de Almeida and Ramos Pereira 2017; Rheingantz et al. 2017). The most consumed fish belong to the families Cichlidae, Anostomidae, Characidae, Loricariidae, and Pimelodidae (Rheingantz et al. 2017). Crustaceans are mainly represented by prawns and crabs (Casariego-Madorell et al. 2008; Rheingantz et al. 2012). A small part of the diet includes insects and mollusks, and their presence varies seasonally (Casariego-Madorell et al. 2008; Carvalho-Júnior et al. 2010; Quadros and Monteiro-Filho 2001; Rheingantz et al. 2011). Tetrapods are also opportunistically consumed; these include small mammals, amphibians, birds, and reptiles (Passamani and Camargo 1995; Gallo-Reynoso et al. 2008; Platt and Rainwater 2011; Santiago-Plata et al. 2013). There is also evidence that otters occasionally eat fruits (Quadros and Monteiro-Filho, 2000, 2001; da Silva et al. 2012). Neotropical otters are opportunistic mammals, showing wide geographic and seasonal plasticity (Gallo-Reynoso 1989; Casariego-Madorell et al. 2008; Briones-Salas et al. 2013; Rheingantz et al. 2017), and this plasticity is also evident in their diet, although fish is their preferred food (Gallo-Reynoso 1986; de Almeida and Ramos Pereira 2017; Rheingantz et al. 2012, 2017).

de Ferran et al. (2024) recently demonstrated, through a phylogenomic analysis of ultraconserved elements, that the Neotropical otter is divided into two species. *Lontra longicaudis* (Olfers, 1818) occurs throughout South America, from the cis-Andean region in south-central Colombia, Venezuela, and Ecuador, through Brazil to northern Argentina, while *Lontra annectens* (Major, 1897) occurs in Mexico, throughout Central America, and extends to the southernmost limit in the trans-Andean region of Colombia, Venezuela, and Ecuador (de Ferran et al. 2024). In Mexico, *L. annectens* is primarily found in tropical areas from southern Tamaulipas to the southwestern Yucatán Peninsula on the Gulf of Mexico side, and from Sonora to Chiapas on the Pacific side (Gallo-Reynoso 1989; Eisenberg and Redford 1999; Perini et al. 2009; Aranda 2012). This taxonomic change could present significant challenges to understanding the ecology of these species individually. For example, several references that cite *L. longicaudis* actually refer to *L. annectens*. However, we will use the term "Neotropical otters" to refer to both species.

We identified a population of *L. annectens* with feeding habits that differ from the known pattern of the species. Therefore, this study analyzes the composition of the diet of this population and its likely consequences on feeding behavior.

Methods

This study was carried out on the El Despoblado River near the municipality of Villa Comaltitlán in southern Chiapas (15°12'27.0"N, 92°33'51.6"W). The local vegetation includes remnants of high tropical forests surrounded by agricultural lands. The river is bordered by riparian vegetation, composed mainly of *Ficus insipida*, *Trichilia havanensis*, *Castilla elastica*, as well as tulares in some parts of the river. There are rocks on the banks and in the middle of the river. The region has a warm and humid climate with heavy summer rains with a maximum temperature in May (29.8 °C), an average of 28 °C from August to November, and the lowest temperature in January (27.02 °C). (INEGI 1985).

Monthly visits were carried out from April 2018 to April 2019, during which approximately 16 km of riverbank was surveyed to collect otter scats. The otter scats were identified by scats size, shape, color, and odor following Aranda (2012). Most scats were found on rocks both in the middle of the river and along the riverbanks. Scats were placed in paper bags, and the following data were recorded for each sample: locality, geographic coordinates, content visible to the naked eye, measurements, date of collection, and sample number. In the laboratory, samples were weighed and placed in beakers with soap and water to separate the contents and fat and neutralize any bacteria. A stereomicroscope was used to identify the food components to the lowest possible taxonomic level in each scats sample using identification guides (Ramos 1997; Ramos and Echeverria 2014) and by comparison with specimens of fish, crustaceans, mollusks, and insects also sampled from the same river, near to scats sites.

For each food item, the percentage of occurrence (PO) was calculated as $PO = FC_i \times 100 / \Sigma F$ where FC_i is the total frequency of occurrence for the prey and F is the frequency per item. The frequency of occurrence (FO) for each item was also calculated as $FO = FE_i / N$ where FE_i is the total number of samples containing the item i and N is the total number of scats samples (Silva et al. 2014; Guerrero et al. 2018). The relative biomass (RB) was calculated as the biomass contribution of each prey expressed as a percentage of total biomass (García and Kittlein 2005; Grajales-Tam and González-Romero 2014). The average biomass of particular vertebrate prey was obtained from a reference collection of prey items captured at the same site where we collected the otter scats.

A comparative analysis was performed by reviewing 21 studies reporting the diet of *L. longicaudis* and *L. annectens*, from which the percentage of occurrence of each food item was extracted (Fig. 1). When the same location was studied for two years, the data for each year were separated and considered in two separate studies. Also, when food items were analyzed at two or more sites in the same study, the information for each site was separated and each one was considered a different study. We excluded studies in which food-composition data could not be converted into a percentage of occurrence.

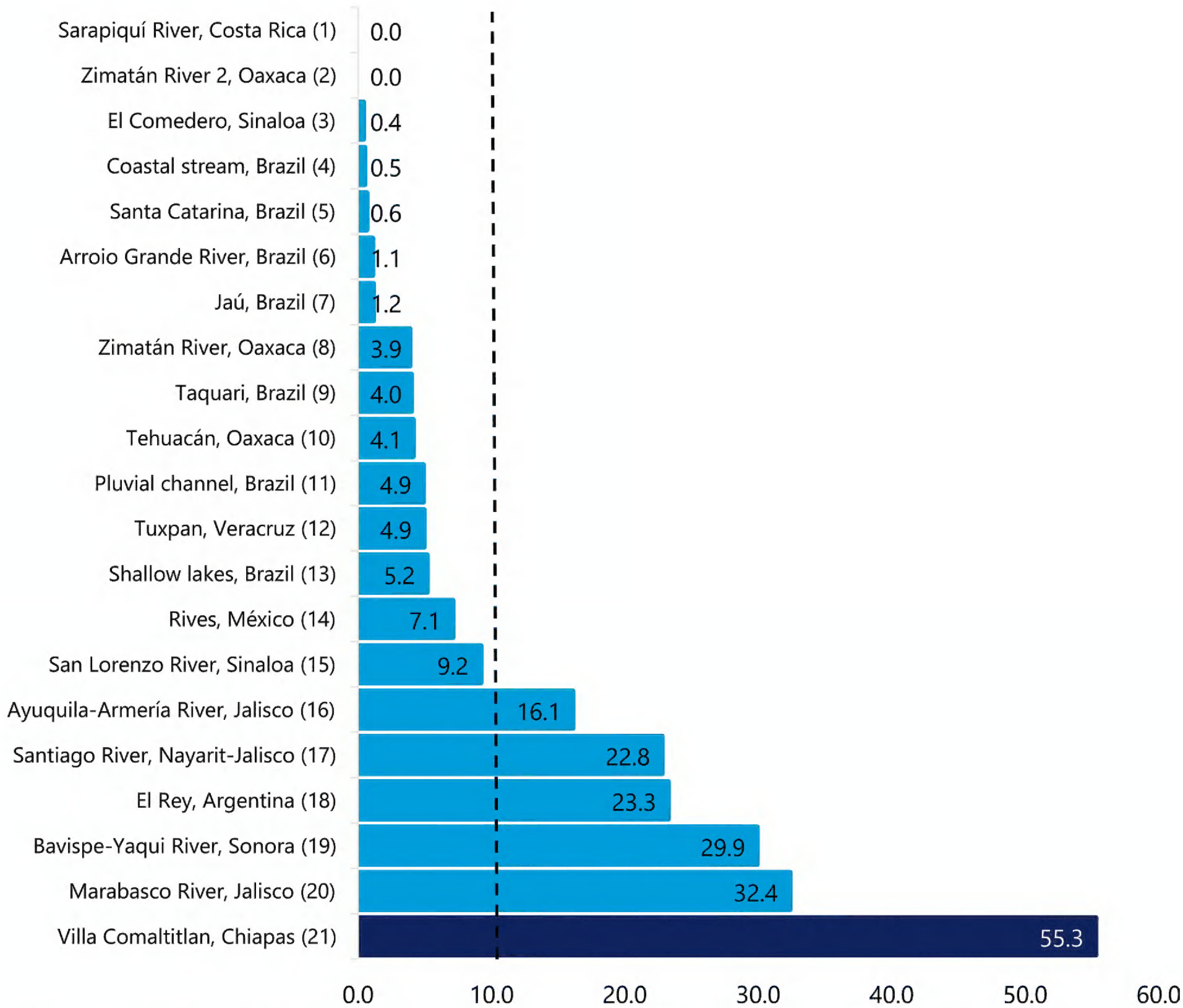

Figure 1. Insects in the diet of Neotropical otters in the Americas (both *Lontra longicaudis* and *L. annectens*), ordered by percentage of occurrence. The dotted line indicates the average number of insects consumed by the otters (11.3%). Spínola and Vaughan 1995 (1), Briones-Salas et al. 2013 (2, 8), García-Silva et al. 2021 (3, 15), Marques Quintela et al. 2012 (4, 11, 13), Quadros and Monteiro-Filho 2001 (5), Souza et al. 2013 (6), Silva et al. 2013 (7), Kasper et al. 2008 (9), Duque-Dávila et al. 2013 (10), Grajales-García et al. 2019 (12), Gallo-Reynoso 1997 (14), Brito-Ríos et al. 2022 (16, 20), Guerrero et al. 2018 (17), Chemes et al. 2010 (18), Rangel-Aguilar and Gallo-Reynoso 2013 (19), this study (21).

Results

A total of 63 scats of *L. annectens* were collected. The diet includes three main groups: insects, fish and crustaceans. The most frequent food item was dobsonfly larvae, (Insecta, Megaloptera) with a PO of 55.3% and a FO of 91.3%. Hellgrammites (Fig. 2), which are larvae of dobsonflies of the genus *Corydalus* Latreille, 1802, were recorded in 51 of the 63 samples. Of the scat samples containing insects, 52% included only dobsonfly larvae (n = 26), while 48% also included fish and crustaceans (n = 25). These scats contained 4 to 13 dobsonfly larvae, with an average of eight larvae per otter scat. The second most important group consumed by otters was fish, with a PO of 34.2% and a FO of 56.5%. The consumed fish belonged to the families Characidae (18.1%), Ictaluridae (9.1%), and Atherinopsidae (7.0%). Crayfish of the family Pseudothelphusidae

Figure 2. Sample of the diet of the *Lontra annectens* in Villa Comaltitlán, Chiapas, Mexico **A** scats with hellgrammites (Insecta: Megaloptera) **B** hellgrammites collected in the study area. Scale bar: 10 mm.

(Crustacea, Decapoda) showed a PO of 10.5% and a FO of 17.4% and were the least abundant group. The dietary importance of dobsonfly larvae was also demonstrated by the percentage of biomass consumed by otters, with dobsonflies accounting for about half of the biomass and fish and crayfish just over a quarter each (Table 1).

Discussion

Neotropical otters are generalist carnivores with opportunistic habits (Rheingantz et al. 2012; 2017; Brito-Ríos et al. 2022), which easily change their diets and adapt to variable environmental conditions (Rangel-Aguilar and Gallo-Reynoso 2013; Rheingantz et al. 2017; García-Silva et al. 2021). Fish are their main prey on both continental and local scales (Gallo-Reynoso 1997; Gori et al. 2003; Rheingantz et al. 2017). Alternative prey tends to increase when the abundance of fish decreases. However, in our study, the diet mainly consisted of insects and was supplemented by fish and crustaceans, which is not consistent with the general food composition in the diet of Neotropical otters.

Insects are common in the diet of the Neotropical otters, ranking fourth in most studies. However, in some studies, they were reported as the second most important food item after fish (n = 4 of 21) (Gallo-Reynoso et al. 2008; Chemes et al. 2010; Guerrero et al. 2018; Brito-Ríos et al. 2022). In contrast, insects were absent from the diet in some studies (Spinola and Vaughan 1995; Louzada-Silva et al. 2003; Briones-Salas et al. 2013), whereas in others they were found in very small percentages. In such cases, it has been suggested that insect intake may be indirect, meaning the insects were present in the gut contents of fish consumed by otters (Quadros and Monteiro-Filho 2001). In *L. annectens*, the

Table 1. Diet of *Lontra annectens* of the El Despoblado River near Villa Comaltitlán, in southern Chiapas. The diet is shown as a frequency of occurrence (FO), the percentage of occurrence (PO), and relative biomass (RB).

Taxon	FO	PO%	RB%
Arthropods			
Megaloptera: *Corydalus*	**91.3**	**55.3**	**42.9**
Decapoda			
Pseudothelphusidae	**17.4**	**10.5**	**29.2**
Fish	**56.5**	**34.2**	**27.9**
Characidae	78.6	18.1	
Ictaluridae	34.8	9.1	
Atherinopsidae	8.7	7.0	

highest percentage of insects consumed was recorded as 32.4% in the Marabasco River, Jalisco (Brito-Ríos et al. 2022), 29.9% in the Bavispe-Yaqui River, Sonora (Rangel-Aguilar and Gallo-Reynoso 2013), and 22.8% in the Santiago River, Jalisco (Guerrero et al. 2018). In *L. longicaudis*, the highest percentage was 23.3% in the El Rey National Park, Argentina (Chemes et al. 2010) (Fig. 1). We found that more than half of the otters' diet in the El Despoblado River consists of insects, a much higher value than the average percentage of insects in otter diet, which is less than 12% (Fig. 1).

The consumption of insects by *L. annectens* is probably related to the time of year. In some places, otters consume more insects in the dry season (Gallo-Reynoso 1996; Macías-Sánchez and Aranda 1999), while they consume insects preferentially in the rainy season in other places (Rangel-Aguilar and Gallo-Reynoso 2013). However, although otters increase their consumption of insects at some times of the year, insects are never the main food source, not even in the season of peak insect consumption; in general, otters feed mainly on fish, regardless of the season (Chemes et al. 2010; Rangel-Aguilar and Gallo-Reynoso 2013; Guerrero et al. 2018; Brito-Ríos et al. 2022;). In our study, most scats containing insects were collected in the rainy season (June; n = 31); however, contrary to previous studies, insects were the main food source for otters at this time, above even fish and crustaceans. Further studies are needed in this river to determine whether this high consumption of insects is due to seasonality or if this is an isolated population of otters that consume the most abundant food resource.

A wide variety of insects are consumed by Neotropical otters, including beetles (Coleoptera) and hymenopterans (Hymenoptera), the main groups in the otter diet, followed by grasshoppers (Orthoptera) in a lower proportion (Gallo-Reynoso 1997; Chemes et al. 2010; Marques Quintela et al. 2012; Rangel-Aguilar and Gallo-Reynoso 2013; Souza et al. 2013; Guerrero et al. 2018; García-Silva et al. 2021). Cockroaches (Blattodea), flies (Diptera), dragonflies and damselflies (Odonata), and cicadas and leafhoppers (Homoptera) have also been found (Quadros and Monteiro-Filho 2001; Chemes et al. 2010; Rangel-Aguilar and Gallo-Reynoso 2013; Guerrero et al. 2018). Finally, insects only occasionally consumed include (Lepidoptera), hemipterans, stoneflies (Plecoptera), caddisflies (Trichoptera), and dobsonflies (Megaloptera) (Kasper et al. 2008; Chemes et al. 2010; Duque-Dávila et al. 2013; Rangel-Aguilar and Gallo-Reynoso 2013). Dobsonflies have been recorded as otter prey only three times and in low proportions: 3.6%

in *L. annectens* in Oaxaca, Mexico (Duque-Dávila et al. 2013), 4.0% in *L. longicaudis* in Taquari Valley, Brazil (Kasper et al. 2008), and 5.7% in the Pomba River, Brazil (da Silva et al. 2012). Dobsonflies (Megaloptera) are flying insects in the adult stage, but larvae are aquatic and can live underwater for 1–3 years before pupating (McCafferty and Provonsha 1983; Mangan, 1994; Evans and Neunzig 1996; Anderson 2003). In tropical regions such as Chiapas, the larvae are probably more abundant in the rainy season, and otters feed preferentially on them.

In general, Neotropical otters prefer to feed on slow-moving prey with limited escape abilities (Pardini 1998; Quadros and Monteiro-Filho 2001; Rheingantz et al. 2012, 2017). This is true for hellgrammites, which spend most of their time under rocks (McCafferty and Provonsha 1983; Mangan 1994; Evans and Neunzig 1996; Anderson 2003). Although otters probably invest considerable time and energy in capturing hellgrammites, the nutritional benefit of consuming these larvae can be high. Insects provide otters with a large number of amino acids, proteins, and vitamins (Oonincx and Finke 2021), in addition to providing a balanced content of essential macronutrients (Coogan et al. 2014; Erlenbach et al. 2014; Gunther et al. 2014; Costello et al. 2016). Larvae, in particular, may represent a higher nutritional value because they have high fat content, and their structures are easier to digest than those of adults due to the lesser amount of chitin in the larval exoskeleton (McCafferty and Provonsha 1983; Redford and Dorea 1984; Mangan 1994; Rawlins and Handasyde 2002; Anderson 2003; Cantú-Salazar et al. 2005).

We document that otters of the species *L. annectens* are opportunistic carnivores with flexible diets that consume food items according to their availability, abundance, and behavior of their prey (Reid et al. 1994; Clavero et al. 2003; Alarcon and Simões-Lópes 2004). When the main prey is either in lower densities or absent, otters display opportunistic behavior and consume prey that is not normally common or that usually occurs in low abundance in the diet (Clavero et al. 2008; Day et al. 2015).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.

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